Diversity and biogeography of deep-ocean sea anemones (Cnidaria: Anthozoa: Actiniaria)

A Senior Honors Thesis

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by

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Abstract

The deep sea and its fauna have been surveyed for over a century, but the ecosystems within had not been explored until the recent advent of maneuverable submersible vessels capable of deep diving. Historically, deep sea animals were blindly collected, poorly preserved, and under-described, leaving modern scientists little information on their attributes or ecology. We wanted to examine the relationship between deep ocean sea anemones and sites of hydrothermal activity. Specifically, we sought to identify taxa as potential vent fauna based on their geographic location, especially those collected without knowledge of their benthic environment. Using modern information on benthic topography and geology, we identify eight confirmed vent species and seven potential vent species from among forty-seven species of sea anemones in the deep Pacific Ocean. All of the confirmed vent species are known from a single vent or vent system, and all belong to different genera. Given this striking degree of endemicity, exploration of the vents and vent systems from which sea anemone diversity is undocumented is likely to be fruitful in terms of the discovery of new species and genera of Actiniaria.

Alvinactis reu gen., sp. nov is a sea anemone which exemplifies the wealth of deep-ocean species to be discovered. We describe this novel genus and species from recent collections that targeted the diversity of fauna at the deep sea hydrothermal vents of the eastern North Pacific Ocean. The combination of characters in *Alvinactis reu* is unique among currently known genera of Mesomyaria; most notable among its external features is a belt of verrucae and cinclides in the distal column. We assess the placement of *Alvinactis* and evaluate taxonomic features used to distinguish groups within Actinostolidae Carlgren, 1893 and Actinoscyphiidae Stephenson, 1920 with a cladistic analysis of morphological characters. Phylogenetic analysis reveals that *Alvinactis* and several genera previously ascribed to Actinostolidae belong in Actinoscyphiidae. Morphological evidence fails to support monophyly of Actinostolidae, but does support monophyly of the previously proposed subfamily Actinostolinae.

Biogeographic review of sea anemones (Cnidaria: Anthozoa: Actiniaria) endemic to the deep Pacific Ocean and their relationship to major sites of hydrothermal vents

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Introduction

Hydrothermal vents are a relatively recently discovered habitat, first described by geologists in 1976. Hydrothermal vent fields are usually found at seafloor spreading centers, which occur at mid-ocean ridges. At these locations, volcanic activity between neighboring tectonic plates forms new oceanic crust. The Pacific Ocean contains several plates, which produce hydrothermal vents where they come in contact. At these oceanic fissures, geothermally-heated seawater, infused with dissolved minerals and heavy metals, emerges in concentrated plumes at up to 400° C (Van Dover et al. 2006). More fascinating than the finding of the geological processes of vents was the discovery of unique vent communities. Dense communities of organisms adapted to the extreme temperature and high mineral content were found surrounding the vents. Hydrothermal vent communities are unusual in that organisms there depend on primary production by chemosynthetic autotrophs, such as sulfur and methane-fixing bacteria, instead of photosynthetic autotrophs. Energy derives not from sunlight, but instead from the oxidation of reduced compounds. Chemosynthetic bacteria provide energy that allows for high diversity and abundance at vents, when compared to the deep seafloor in general. The discovery of vents showed that diverse, complex ecosystems containing macroscopic multicellular animals could be supported by microbial chemosynthetic primary production (Van Dover et al. 2006).

Hydrothermal vents present unique challenges to their inhabitants in terms of reproduction and dispersion. Although a vent field may be active for a long period of time,

individual vents are often short-lived phenomena. The movement of molten rock beneath the surface can divert hydrothermal circulation without overflowing onto the seafloor (Van Dover et al. 2006). In such an event, a vent may lose its hydrothermal connection and cease active production, resulting in the death of all its inhabitants. At the same time, flow may emerge elsewhere, creating new vent habitats. It is believed that vents are only active for a number of months to years (Van Dover 2000). Therefore, it is important for vent taxa to transmit progeny to another hydrothermal vent within a short period of time. Most vent species do not broadcast spawn, but their larvae may be competent for long periods, increasing the chances of successful colonization (Tyler and Young 2001). These reproductive pressures are even greater for sessile organisms, such as sea anemones, which cannot migrate as adults. In addition to the difficulty of migration to suitable habitats, relatively low larval dispersal may contribute to high endemicity (Tyler and Young 2001).

Over the past 150 years, with collections being most intense from about 1880 to 1930, the benthic marine fauna was collected during oceanographic expeditions that blindly dredged and trawled the deep sea. These naturalists did not have detailed knowledge about the submarine environments which they surveyed, let alone an awareness of the existence of hydrothermal vents. Therefore, descriptions of animals lacked important ecological information that is only knowable through visual exploration of their habitats. Since the discovery of vents in 1976, scientists have explored a limited number of them, often collecting organisms using maneuverable deep-submersible vessels. Yet a mere 1.6% of the total identified vent species are sea anemones, indicating a severe lack of information regarding this group of organisms (López-González 2007). Sea anemones are usually found at vents, but are often not studied because of the lack of a specialist (Daly and Rodríguez, personal observation). Although data are limited, it is believed that most vent anemones are

part of a single evolutionary radiation, as they constitute a monophyletic group (Rodríguez et al. 2008).

Since 1976, scientists have located at least ninety-eight major hydrothermal vent fields, across the Atlantic, Indian, and Pacific Oceans, and the Mediterranean Sea. Seventy-nine of these are located in the Pacific Ocean (Fig. 1), where surveying has been most intense. Still, our knowledge of hydrothermal vent locations is limited, since surveying of the deep ocean benthos is a costly undertaking. In light of recent advances, it is possible to compare historical information on deep ocean sea anemones and modern knowledge of the location and nature of hydrothermal vents. We wanted to examine the relationship between deep ocean sea anemones and sites of hydrothermal activity. Specifically, we sought to identify taxa as potential vent fauna based on their geographic location, especially those collected without knowledge of their benthic environment.

Materials and Methods

Taxonomic, distributional, and bathymetric information on all deep ocean (at least 1000 m in depth) Pacific sea anemones were gathered primarily from an online database that contains a catalogue, bibliography, and distribution map for all extant sea anemone species. This database, known as Hexacorallians of the World (Fautin 2007), is a compilation of information on all extant hexacorallians, including taxonomy, taxon synonymy, taxonomic status, nomenclature, type specimens, type locations, published geographic distribution, and bibliographic references for all known species. It also includes interactive world maps, arranging specimens by latitude and longitude coordinates. The database includes cnidarians of the orders Actiniaria, Antipatharia, Ceriantharia, Corallimorpharia, Ptychodactiaria, Scleractinia, and Zoanthidea. For this study we were focused on order Actiniaria, sea anemones in the strictest sense.

For information that could not be elicited from Hexacorallians of the World, primary (e.g. – original species descriptions) and secondary (e.g. – López-González 2007) literature were consulted. The locations of hydrothermal vents were gathered from the literature (e.g. – Desbruyéres 2007).

Our search was limited to species found in the Pacific Ocean. To the north, boundaries included Alaska and eastern Russia; we did not consider anything from above the Arctic Circle (66° 33'39"), since the land bridge prevents circulation and no hydrothermal systems are known in this region. The eastern boundaries were defined as the western coast of America, and 60° W in the south (roughly from the Falkland Islands south to the tip of the Antarctic Peninsula). The western boundaries were defined as the eastern coast of the Asian continent. In Southeast Asia, the border ran from the Malay Peninsula through the middle of the Indonesian archipelago (along the eastern and northern borders of the Indonesian islands of Sumatra and Java). The southwest was bounded by 115° E (roughly the west coast of Australia and southward to Antarctica). However, we did not consider the waters north of Australia between 115° E and 130° E (roughly between 10° S and 20° S). This decision was made because this body of water circulates more readily with the Indian Ocean than the Pacific Ocean, due to the presence of the Indonesian land masses. This information is summarized in Fig. 1.

We generated a database to incorporate and organize all biogeographic information on Pacific deep-ocean sea anemones, as well as known hydrothermal vents. To test whether these distributions were associated, an interactive digital map of sea anemones and vent/seep locations was created using GoogleEarth. GoogleMaps was utilized to create a Mercator projection and measure distances between vents and sea anemones.

Results

This study yielded an interactive, GoogleEarth-based biogeographic system that can be utilized to elicit ecological information for any given species of Pacific deep ocean sea anemone (Fig. 1). A summary of all sea anemones from the deep Pacific Ocean is shown in Table 1.

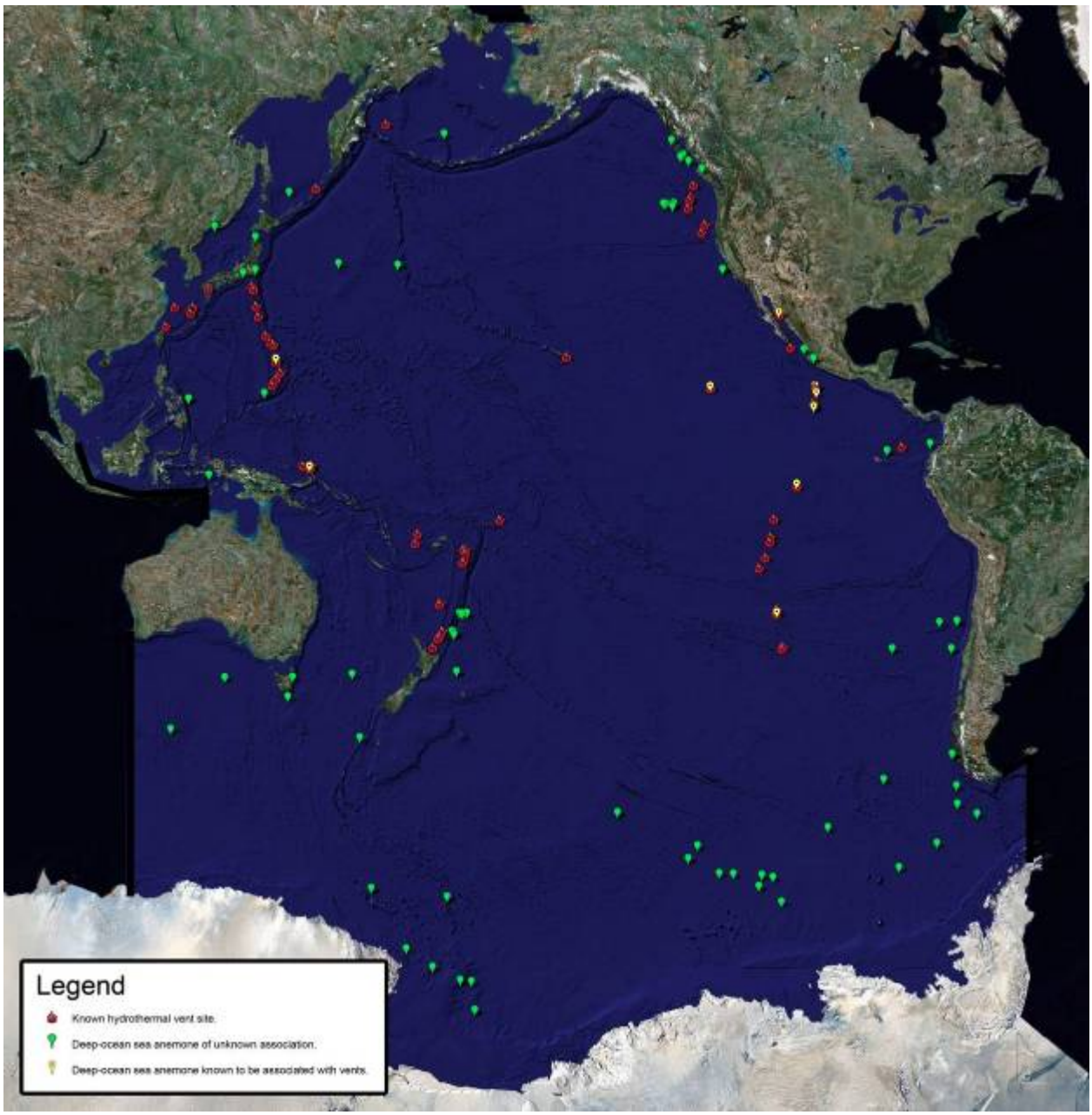

Figure 1. Mercator projection of the Pacific Ocean. Locations of known hydrothermal vents, deep-ocean sea anemones of unknown association, and deep-ocean sea anemones known to be associated with vents are shown in red flames, green flags, and dotted yellow flags, respectively.

Table 1. Sea anemones known from the deep Pacific Ocean.

Family	Genus	Species	Depth Range (m)	Pacific Latitudes (°)	Pacific Longitudes (°)
Actinernidae	*Actinernus*	*elongatus*	4755	-42.7	134.17
			2507-2525	-66.84	164.48
			1647-1665	-51.13	162.04
			1080	-67.5	-179.93
			4575-4813	-64.28	-130.15
			1896-1920	-53.11	-75.77
			1500-1666	-53.24	-75.68
Actiniidae	*Bolocera*	*kerguelensis*	3338	-38.1	-88.03
			2022-2060	-74.93	-174.23
			2507-2525	-66.84	164.48
Actiniidae	*Glyphoperidium*	*bursa*	1210	-73.24	-177.19
			1883-1890	-72.44	177.14
Actinoscyphiidae	*Actinoscyphia*	*plebeia*	1238	-38.13	-75.88
			1500-1666	-53.24	-75.68
			2782-2827	-59.97	-70.62
Actinostolidae	*Actinostola*	*crassicornis*	2022-2060	-74.93	-174.23
Actinostolidae	*Anthosactis*	*excavata*	2515	-33.7	-78.3
Actinostolidae	*Bathydactylus*	*kroghi*	8210-8300	-35.27	-178.67
Actinostolidae	*Ophiodiscus*	*annulatus*	3950	-33.52	-74.72
Actinostolidae	*Ophiodiscus*	*sulcatus*	2515	-33.7	-78.3
Actinostolidae	*Sicyonis*	*erythrocephala*	2377	-42.63	148.14
Actinostolidae	*Sicyonis*	*tubulifera*	3429	34.62	140.53
Actinostolidae	*Synsicyonis*	*elongata*	5304	35.37	169.88
Actinostolidae	*Stomphia*	*selaginella*	1565-1674	-71.27	171.67
Actinostolidae	*Tealidium*	*cingulatum*	3292	-50.02	123.07
Bathyphelliidae	*Bathyphellia*	*australis*	4575	-62.88	-78.81
			3954-4042	-67.91	-110.93
			4575	-58.96	-74.65
			4319	-59.83	-144.78
			3200-3259	-59.82	-144.78
Bathyphelliidae	*Daontesia*	*mielchei*	7250	-5.43	130.97
Edwardsiidae	*Edwardsia*	*arctica*	2300	41.64	132.13
Galatheanthemidae	*Galatheanthemum*	*hadale*	10190	10.22	126.72
			10160-10210	10.32	126.65
			9790	10.33	126.68
Hormathiidae	*Amphianthus*	*bathybium*	4206	35.68	157.7
			5304	35.37	169.88
Hormathiidae	*Amphianthus*	*margaritaceus*	3500	46.68	147.47
Hormathiidae	*Chondrophellia*	*coronata*	1238	-38.13	-75.88
Hormathiidae	*Hormathia*	*spinosa*	3429	34.62	140.53
Hormathiidae	*Hormathia*	*lacunifera*	1080	-67.5	-179.93
			1000-1750	-42.15	160.51
Hormathiidae	*Paracalliactis*	*involvens*	1355	1.05	-80.25
Hormathiidae	*Paraphelliactis*	*pabista*	1829	51.72	-131.23
			2195	50.91	-130.1
			1920	53.55	-133.63
			2430	51.45	-131.79

			1830	49.88	-127.38
Hormathiidae	*Stephanauge*	*hyalonematis*	1485	-0.4	-89.1
Isanthidae	*Eltaninactis*	*infundibulum*	2610-2668	-41.74	-177.99
Liponematidae	*Liponema*	*multipora*	2610-2668	-41.74	-177.99
			2897-2907	-73.32	-174.87
			2840-3001	-45.52	147.22
			3429	34.62	140.53
Liponematidae	*Liponema*	*brevicornis*	1019	54.3	179.5
Sagartiidae	*Antheomorphe*	*elegans*	5304	35.37	169.88
Actiniaria *incerta sedis*	*Polyopis*	*striata*	3950	-33.52	-74.72
Actiniaria *incerta sedis*	*Aulorchis*	*paradoxa*	3950	-33.52	-74.72
Actinernidae	***Actinernus***	***robustus***	**3429**	**34.62**	**140.53**
Actinostolidae	***Actinostola***	***callosa***	**1485**	**-0.4**	**-89.6**
Actinostolidae	***Anthosactis***	***nomados***	**4100**	**34.72**	**-123.1**
			4100	**34.67**	**-123.05**
			4100	**34.75**	**-123.03**
			4100	**34.77**	**-123.13**
			4100	**34.7**	**-123.13**
			4100	**34.68**	**-123.18**
			3700	**45.09**	**-133.18**
			3900	**45.03**	**-134.7**
			3900	**45.06**	**-134.75**
			3932	**45.02**	**-135.23**
			3990	**45.03**	**-135.39**
Actinostolidae	***Hadalanthus***	***knudseni***	**6660-6720**	**-35.85**	**-178.52**
			3443	**18.35**	**-104.35**
			3354	**18.34**	**-104.36**
			3795	**20.03**	**-106.29**
Exocoelactiidae	***Exocoelactis***	***tuberosa***	**1033**	**34.12**	**138**
Galatheanthemidae	***Galatheanthemum***	***profundale***	**10630-10710**	**11.32**	**142.34**
			6960-7000	**-32.18**	**-177.32**
			6620	**-32.34**	**-176.9**
			6140-6160	**-32.15**	**-176.58**
			5850	**-32.17**	**-175.9**
			7630	**-35.33**	**-178.92**
			8210-8300	**-35.27**	**-178.67**
			6660-6720	**-35.85**	**-178.52**
			4575-4813	**-64.28**	**-130.15**
			4682	**-63.12**	**-128.19**
			4709	**-65.57**	**-123.71**
			4758-4804	**-65.62**	**-120.86**
			4773	**-65.72**	**-114.96**
			4676	**-66.67**	**-115.6**
			4789-4795	**-65.92**	**-112.71**
			4868-4923	**-61.36**	**-101.37**
			5087-5124	**-56.22**	**-89.84**
			4529-4548	**-65.08**	**-86.66**
			4209	**-56.94**	**-74.81**
Hormathiidae	***Monactis***	***vestita***	**3990**	**45.03**	**-135.39**
			3932	**45.02**	**-135.23**

			3900	45.06	-134.75
			3900	45.03	-134.7
			3900	45.09	-134.72
			3717	44.68	-133.44
			3700	45.09	-133.18
Actinoscyphiidae	*Paranthosactis*	*denhartogi*	2025	27.02	-111.41
			2020	27.01	-111.41
Actinoscyphiidae	*Pacmanactis*	*hashimotoi*	1674	-3.73	151.67
			1627	-3.73	151.67
Actinostolidae	*Actinostola*	sp.*	~2635	12.83	-103.95
Actinoscyphiidae	*Alvinactis*	*reu*	2600	12.7114	-125.6136
Actinoscyphiidae	*Cyananthea*	*hydrothermala*	2000	12.8	103.95
Actinoscyphiidae	*Marianactis*	*bythios*	3640	18.21	144.71
			3660	18.18	144.72
			3660	18.21	144.71
Boloceroididae	*Boloceroides*	*daphneae*	2565	8.63	-104.21
			2622	12.81	-103.94
			2483	11.41	-103.69
			2560	8.61	-104.21
			2637	12.81	-103.95
Hormathiidae	*Chondrophellia*	sp.†	~2635	12.83	-103.95
			~2735-3752	-7.35	-107.78
			~2235	-32	-111.92

Legend

Deep-ocean sea anemone of unknown association
Deep-ocean sea anemone of unknown association, within 250 km of a vent
Deep-ocean sea anemone known to be associated with vents

**Actinostola* of unidentified species (López-González and Segonzac 2006a); probably actually a Hormathid.
†*Chondrophellia* of undescribed species (López-González and Segonzac 2006b).

Since nearly all deep ocean sea anemones were originally collected without detailed knowledge of their habitat, this descriptive research allowed us to use distributional, topographical, and geological information to draw inferences about the environments and ecology of poorly-described sea anemones. It also enabled us to measure distances between hydrothermal vents and known locations of deep ocean sea anemones.

We found 47 unique species from 36 genera and 97 distinct collection localities. Eight of these species (17%) are confirmed from known hydrothermal vents. These species are *Paranthosactis denhartogi*, *Pacmanactis hashimotoi*, *Alvinactis reu*, *Cyananthea hydrothermala*, *Marianactis bythios*, and *Boloceroides daphneae*, as well as two species of

the genera *Actinostola* and *Chondrophellia* which are unidentified and undescribed, respectively. Six of these species (75%) were collected from a single vent and two of these species (25%) collected from a single ridge/vent system. Five of these species (63%) belong to genera found only at vents (vent-endemic).

Thirty-nine species (83%) were of unknown association. Of these species, seven (18%) have been found within 250 kilometers of a known vent. These species are *Actinernus robustus*, *Actinostola callosa*, *Anthosactis nomados*, *Hadalanthus knudseni*, *Exocoelactis tuberosa*, *Galatheanthemum profundale*, and *Monactis vestita*.

Discussion

The vast majority of described deep-ocean sea anemone species are of unknown association (83%). Sea anemone species that are found at vents are known from either a single vent or a single ridge/vent system. This indicates that identified vent sites are under-surveyed, and suggests a high level of endemicity for sea anemones at vents. Further support for high endemicity is the fact that all recognized vent species are from different genera.

We do not agree with López-González and Segonzac (2006a) on their identification of *Actinostola* sp. based on a photograph from a vent at the East Pacific Rise. Species of *Actinostola* have a smooth column (Carlgren 1949), whereas the animal in their photograph has a column bearing cuticle. This specimen more likely belongs to family Hormathiidae (Daly and Rodríguez, personal observation), whose members often bear cuticle on the column and are common in the deep sea (Carlgren 1949; Fautin and Barber 1989). The species identified as *Chondrophellia* sp. is a currently undescribed species (López-González and Segonzac 2006b), likely to belong to a new taxon (Daly and Rodríguez, personal observation).

We identified seven deep ocean sea anemone species from within 250 kilometers of a known vent. Given the relative proximity to vents, these species are potential vent organisms. The specific locations of hydrothermal vents can shift over time as the geological dynamics of mid-oceanic ridges change in both latitude and longitude, and bathymetry (Van Dover 2000). Furthermore, charting by early naturalists was not as precise as modern, satellite-based global positioning systems. These seven species are candidates for further investigation of distribution, ecology, life-history, and morphology to ascertain whether they are actually vent taxa. It would be interesting to return to original dredge and trawl locations and explore the benthos using maneuverable deep submersible vehicles to search for the presence of extant hydrothermal vents or remnants of extinct vents.

If not found to be from vents themselves, these candidate species may be from the vent periphery. Vents contribute inorganic chemicals, such as sulfide, and organic carbon to nearby regions (and indeed the entire global oceanic system). Particulate organic matter (POM) has been documented to spread at least 2 kilometers from vents (Roth and Dymond 1989). However, the impact zone of hydrothermal vent fields has yet to be quantified and the specifics of vent to non-vent benthic coupling are still unclear (Van Dover 2000).

This map facilitates visualization and identification of unsurveyed ocean-floor locations and regions that seem to be lacking Actiniarian fauna. An extremely small portion of the ocean floor has been extensively sampled; the vast majority has yet to be well characterized. For regions of seafloor that have been sampled and clearly lack sea anemones, specific attributes of the habitat may prevent colonization. Furthermore, though a number of hydrothermal vents have been identified, the biodiversity of the great majority of them has not been sampled (Van Dover 2000).

With knowledge of both surface and deep ocean currents, this study has important implications for studies of reproductive distribution. Finally, the methodology of this

research could easily be applied to other groups of deep-sea organisms or to other marine habitats. Cold seeps, another variety of chemosynthetic environment, are a similar habitat to hydrothermal vents. There is a significant amount of taxonomic overlap between the two habitats and some propose that they are "stepping-stone" ecosystems from one site to another in terms of colonization and evolution (Van Dover et al. 2002). Therefore, interesting results could arise from the incorporation of cold seeps into this study. The Atlantic and Indian Oceans, too, bear chemosynthetic environments. These sites could be incorporated into work from the Pacific Ocean. The Atlantic Ocean, in particular, is geologically much younger than the Pacific and therefore we hypothesize that vent fauna in the Atlantic Ocean should be evolutionarily derived from the Pacific and Indian Oceans.

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Morphological phylogeny of family Actinostolidae (Anthozoa: Actiniaria) with a description of a new genus and species of hydrothermal vent sea anemone redefining family Actinoscyphiidae

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Introduction

Sea anemones attributed to the family Actinostolidae dominate in the deep sea and polar waters (Carlgren 1949; Fautin and Barber 1999) and at hydrothermal vents (López-González and Segonzac 2006). The majority of the genera currently placed in it are monotypic (Fautin 2007), suggesting that the taxonomic characters traditionally used to differentiate genera need to be re-assessed. The descriptions of several new monotypic genera in recent decades (Doumenc and Van Praët 1988; Fautin and Hessler 1989; Fautin and Barber 1999; López-González *et al.* 2003, 2005) demonstrate the difficulty of accommodating new taxa in narrowly-defined existing groups, and further argue for a re-evaluation of the family. Furthermore, a synthetic, phylogenetic assessment of Actinostolidae would clarify the relationship between the monotypic genera and large, heterogeneous groups such as the type genus, *Actinostola* Verrill, 1883. However, such an assessment is difficult because the family is likely to comprise a paraphyletic grade or a polyphyletic assemblage rather than a monophyletic group.

Actinostolidae has a long and complex taxonomic history (Table 1). Several members of Actinostolidae were first grouped together by Hertwig (1882) in family Paractidae, which he defined as comprising "Hexactiniae with numerous perfect septa and with very contractile moderately long tentacles, which can be completely covered; circular muscle very strong, mesodermal". In this family, he included *Antholoba* Hertwig, 1882, *Dysactis* Milne Edwards, 1857, *Ophiodiscus* Hertwig, 1882, *Tealidium* Hertwig, 1882, and taxa no longer considered

valid, such as its type genus *Paractis* Milne Edwards & Haime, 1851. Andres (1883) used the name Paractidae for a sub-family of his Actininae, and placed in this group *Paranthus* Andres, 1883, *Paractinia* Andres, 1883, and *Paractis*. Hertwig's (1882) use of the name has priority.

Carlgren (1893) redefined Paractidae and transferred its previous diagnosis to a new family, Actinostolidae, into which he placed *Actinostola* and *Stomphia* Gosse, 1859. Carlgren (1893) defined Actinostolidae as "Actiniaria with pedal disc, with very contractile and moderate long tentacles and usually numerous perfect mesenteries. Pairs of mesenteries of the last cycles (third and forth cycles) irregularly developed, so the mesentery, which retractor muscles are facing the next cycle, is more developed than the other. Radial muscles of oral disc and longitudinal tentacle muscles generally mesogleal. Sphincter mesogleal usually well developed. No acontia or cinclides". Carlgren (1893) also provided a new diagnosis for Paractidae: "Actiniaria with pedal disc, with moderate long tentacles and usually numerous perfect mesenteries. Mesenteries of the same pair regularly developed. Radial muscles of oral disc and longitudinal tentacle muscles generally mesogleal. Sphincter mesogleal usually well developed. No acontia or cinclides". His distinction between the two was based on the development of pairs of mesenteries: in Actinostolidae, the two members of a pair are not identical in size and morphology; in Paractidae, the two members of a pair are identical. Carlgren (1899) subsequently reclassified Actinostolidae and Paractidae as subfamilies of family Paractidae, later adding a third subfamily, Polysiphoniinae Carlgren, 1918. Polysiphoniinae was later removed from Paractidae and reclassified as Exocoelactidae Carlgren, 1925.

Although he used Carlgren's subfamilies, Stephenson (1921) was not sure that the distinctions between them were clear, and did not think that any of them merited the rank of family. In particular, Stephenson (1921) considered Actinostolinae and Paractinae a single,

difficult-to-subdivide group. Carlgren (1927) was unable to determine a valid diagnosis for the type genus *Paractis,* and later (Carlgren 1932) resurrected the family name Actinostolidae for some members of Paractidae.

Recent works by Riemann-Zürneck (1978a) and Fautin and Hessler (1989) changed the definition of the family and reconsidered some features used to differentiate its members. Riemann-Zürneck (1978a) revised the mesomyarian family Actinoscyphiidae Stephenson, 1920, clarifying the distinctions between this group and Actinostolidae. Fautin and Hessler (1989) amended Carlgren's (1949) key to the genera of Actinostolidae, correcting his errors and incorporating new species. In their revised key, Fautin and Hessler (1989) omitted *Cyananthea* Doumenc & Van Praët, 1988 because the sole account of its type species was too fragmentary to evaluate many of the critical features. This genus has been recently re-described and placed in the family Actinoscyphiidae based on its cnidom (Sanamyan and Sanamyan 2007). This redescription of *Cyananthea* highlights the confusion that remains about the circumscription of Actinoscyphiidae and Actinostolidae: Sanamyan and Sanamyan (2007) point out that additional genera that had been described as Actinostolidae are likely to be more appropriately placed in Actinoscyphiidae, but they fail to fully address this issue or formally reassign genera.

We describe *Alvinactis reu* gen., sp. nov. from the East Pacific Rise of the North Pacific Ocean. This new genus has a mesogleal sphincter and lacks acontia, and thus belongs to Mesomyaria. To assess the distinctiveness of *Alvinactis* gen. nov. and to evaluate whether it belongs to Actinostolidae or Actinoscyphiidae, we generated a data matrix of morphological features of genera of Actinostolidae and Actinoscyphiidae. Although morphological attributes may be subject to convergence, preservation artefacts, or other sources of systematic error, these are the only data available for many of these taxa, because most are known only from formalin-fixed museum material. Phylogenetic analysis of this

matrix is used to explore the consistency and information content of various taxonomic features used in classification of Actinostolidae and Actinoscyphiidae, test the monophyly of each family, and identify potentially monophyletic groups within Actinostolidae. This is the first cladistic analysis for members of the actiniarian superfamily Mesomyaria.

Materials and Methods

Specimens were collected during a cruise of the Woods Hole Oceanographic Institution research vessel "Atlantis" using the Deep Submergence Vessel "Alvin". All specimens came from one collection during dive 3941, on 26 November 2003, in the North Pacific Ocean: East Pacific Rise, 12°42.680'N, 103°54.462'W, depth 2600 m. Specimens were collected using Alvin's manipulator arm; at the surface, specimens were placed in chilled water and allowed to relax before being anaesthetized with isotonic magnesium chloride. Pieces of some specimens were fixed immediately in 95% ethanol. The remaining specimens were fixed in 10% seawater formalin and later transferred to 70% ethanol for long-term storage. All specimens were deposited at the Field Museum of Natural History (FMNH).

Preserved specimens were examined whole, in dissection, and as serial sections. Serial sections were prepared using standard paraffin techniques. Histological slides were stained in Masson's trichrome (Presnell and Schreibman 1997). Small pieces of tissue from tentacles, column, pedal disc, mesenterial filaments, and actinopharynx were smeared on a slide; nematocysts in these smears were examined using DIC at 100X magnification. Cnidae terminology follows Mariscal (1974).

The phylogenetic analysis of genera of Actinostolidae is based on a matrix of characters scored from direct observation or descriptions of type species. The characters are those traditionally used to recognize taxa within Actinostolidae, including those features

identified by Carlgren (1949) in his key to the family. Some of these features (e.g., bathymetric range, habitat) are not strictly morphological, but can be interpreted as proxies for physiological attributes. All characters are treated as unordered and weighted equally. Outgroups include four genera classified in more distant groups: the endomyarian *Epiactis* Verrill, 1869 and the acontiarians *Bathyphellia* Carlgren, 1932, *Hormathia* Gosse, 1859, and *Kadosactis* Danielssen, 1890. These species span the diversity of Actiniaria and thus provide a strong test of monophyly of Actinostolidae. We included the mesomyarian *Actinoscyphia* Stephenson, 1920 because it was once included in Actinostolidae (Table 1), and because several taxa originally assigned to Actinostolidae have been hypothesized to be closely related to this genus (Riemann-Zurneck 1978a; Sanamyan and Sanamyan 2007). The character states attributed to the generic exemplars in the analysis were evaluated from direct observation or literature reports of type species, except in the case of *Bathydactylus* Carlgren, 1928. We considered *Bathydactylus krogni* Carlgren, 1956 rather than *Bathydactylus valdiviae* Carlgren, 1928, because the type species of the genus is known only from a single, poorly-preserved specimen. We included three species of *Anthosactis* Danielssen, 1890 because the great heterogeneity of the genus (White *et al.* 1999; Daly and Gusmão 2007) raises concern that the group is not monophyletic. Riemann-Zurneck (1978b) synonymized *Paractinostola* Carlgren, 1928 with *Actinostola*, but recognized that the latter was likely to be a paraphyletic group. We included the type species of the former *Paractinostola*, *Paractinostola bulbosa* Carlgren, 1928, in recognition of the heterogeneity in *Actinostola*. The initial assessment of nematocyst types in the tentacles of *Paranthosactis* was equivocal (López-González *et al.* 2003); upon reconsideration of their material and photographs, we find that the nematocysts called microbasic *b*-mastigophores by López-González *et al.* (2003) are holotrichs similar in size and morphology to those seen in the tentacles of *Alvinactis* gen. nov. Other comparative material examined includes *Marianatis bythios* Fautin & Hessler,

1989 deposited at the US National Museum of Natural History (USNM 84401, 84402), *Bathydactylus krogni* and *Epiparactis dubia* Carlgren, 1928 deposited at Zoological Museum in Copenhagen, and *Anthosactis pearseae* Daly & Gusmão, 2007 deposited at the California Academy of Sciences (CAS 174323-174325) and the US National Museum of Natural History (USNM 1096705, 1096706).

The final matrix of 41 characters (Appendix 1 and 2) was analyzed in NONA (Goloboff 1999), using Winclada (Nixon 1999) to initiate 50 rounds of TBR branch swapping. Further rounds of swapping were not recommended by the results of the initial searches. We present the strict consensus of the equally parsimonious trees with Bremer support (Bremer 1994) calculated for all clades appearing in the consensus. The character optimizations discussed are those features that can be placed unambiguously at a particular node. Numbers in the text, on Fig. 1, and in Appendix 2 refer to the characters of Appendix 1.

Carlgren (1949) used the ranks "tribe" and "subtribe" to refer to groups between suborders and families. We have corrected this misapplication of ranks in our treatment of the taxonomy of *Alvinactis reu* gen., sp. nov. We have based our diagnoses of higher taxa on those of Carlgren (1949) and Riemann-Zürneck (1978a), altering them to be parallel and telegraphic; more substantive changes are indicated in italics.

Results

Phylogenetic analysis recovered 22 trees of L=166 (CI=0.30, RI=0.59). The strict consensus of these (Fig. 1) includes two main clades. One of these is a large clade that includes *Actinostola*, *Antholoba*, *Anthosactis janmayeni* Danielssen, 1890, *Cnidanthus* Carlgren, 1927, *Hormosoma* Stephenson, 1918, *Ophiodiscus*, *Paractinostola*, *Parasicyonis* Carlgren, 1921, *Pycnanthus* McMurrich, 1893, *Sicyonis* Hertwig, 1882, *Stomphia*,

Synsicyonis Carlgren, 1921, and *Tealidium*; this roughly corresponds to Carlgren's subfamily Actinostolinae. Henceforth, we refer to this clade as "Actinostolina".

The other main clade includes the remaining genera previously attributed to Actinostolidae, *Actinoscyphia*, and the outgroups *Bathyphellia, Hormathia,* and *Kadosactis,* which nest among members of Actinostolidae. This clade comprises two smaller clades: one includes the acontiate outgroups together with *Bathydactylus* and *Hadalanthus* Carlgren, 1956; the second includes *Actinoscyphia*, *Epiparactis*, and the taxa from chemosynthetic habitats (Fig. 1). The membership of this second clade corresponds closely to Actinoscyphiidae sensu Sanamyan and Sanamyan (2007); we refer these taxa to this family. All taxa from hydrothermal vents and cold seeps (*Alvinactis* gen. nov., *Cyananthea*, *Maractis*, *Marianactis*, *Pacmanactis* López-González *et al*. 2005, and *Paranthosactis*) form a clade without consistent internal resolution. This chemosynthetic habitat clade, hereafter called Chemosynthina, is strongly supported by six morphological characters (#s 5, 6, 9, 17, 26, 31) and two additional ones referring to the habitat (#s 38, 39). The three species of *Anthosactis* do not group together.

Order Actiniaria Hertwig, 1882

Suborder Nynantheae Carlgren, 1899

Superfamily Mesomyaria Stephenson, 1921

Family Actinostolidae Carlgren, 1893

Diagnosis. *Nynantheae with basilar muscles and mesogleal marginal sphincter*; column commonly smooth, rarely tuberculate or with papillae. Tentacles regularly arranged, their aboral sides sometimes with nematocysts batteries, sometimes thickened. Mesenteries not divisible into macro- and micro-cnemes. Younger mesenteries not bilaterally arranged.

Retractor muscles diffuse, rarely circumscribed. No acontia. *Cnidom: Gracile spirocysts, basitrichs, and microbasic b- and p-mastigophores.* (Modified from Carlgren 1949).

Remarks. Carlgren (1949) listed the authorship of Actinostolidae as Carlgren, 1932 but the family was erected by him in 1893 (Table 1).

Included genera. *Actinostola*; *Antholoba*; *Anthosactis*; *Antiparactis* Verrill, 1899; *Bathydactylus*; *Cnidanthea* Carlgren, 1956; *Cnidanthus*; *Hadalanthus*; *Hormosoma*; *Ophiodiscus*; *Paranthus*; *Parasicyonis*; *Pseudoparactis* Stephenson, 1920; *Pycnanthus*; *Sicyonis*; *Stomphia*; *Synsicyonis; Tealidium.*

Family Actinoscyphiidae Stephenson, 1920

Diagnosis. *Nynantheae with basilar muscles and mesogleal marginal sphincter*. Pedal disc *flat*, sometimes small, grasping. Column commonly smooth, *often with distal row of cinclides and sometimes verrucae*. Tentacles usually marginal on wide oral disc, their aboral sides sometimes thickened. Oral disc sometimes lobed. *Mesenteries not divisible into macro- and micro-cnemes*. At least six pairs of perfect and fertile mesenteries. Retractor muscles diffuse and weak. Longitudinal muscles of the tentacles ectodermal. No acontia. Cnidom: *Robust and gracile* spirocysts, basitrichs, *holotrichs*, and microbasic *p*-mastigophores. (Modified from Riemann-Zürneck 1978a).

Remarks. Riemann-Zürneck (1978a) resurrected Actinoscyphiidae primarily based on Schmidt's (1972) classification of types of cnidae. Thus, Riemann-Zürneck (1978a) characterizes Actinoscyphiidae as having "*p*-rhadoids B" and lacking "*p*-rhadoids A". Schmidt's distinction between the categories "*p*-rhadoids A/*p*-rhadoids B" roughly corresponds with Mariscal's distinction between "microbasic *p*-mastigophores/amastigophores". Nomenclatural issues aside, although these types are

certainly different in ultrastructure (shaft and tubule spination), accurate recognition of their distinctiveness requires observing them in a discharged state under SEM. To use all of Schmidt's subdivisions of *p*-mastigophores is necessary to observe the fine details of spine length, density and angle of attachment which are important characters in this system (England 1991; Östman 2000). Using the ultrastructure of *p*-mastigophores, Schmidt (1972, 1974) grouped mesomyarian families into "Early" and "Late" Mesomyaria). However, his distinction was based on examination of relatively few species; these types of nematocysts have not been distinguished for most of the genera. Furthermore, many actiniarian families are polyphyletic (Daly *et al.* 2008), making combining them into groups especially problematic. The phylogenetic interpretation of morphological differences among nematocyst types is not clear. Because molecular evidence does not support Schmidt's (1972, 1974) distinction between "Early" and "Late" Mesomyaria (Daly *et al.* 2008), attributing high phylogenetic significance to the distinction between A or B *p-mastigophores* may be unwarranted. Given the current lack of clarity about the generality and applicability of this character to many taxa, and its dubious value as a phylogenetic feature, we prefer not to include these differences in the definition of the families.

Included genera. *Actinoscyphia*, *Alvinactis* gen. nov., *Cyananthea*; *Epiparactis* Carlgren, 1921; *Maractis* Fautin & Barber, 1999; *Marianactis* Fautin & Hessler, 1989; *Pacmanactis*; *Paranthosactis*.

Genus *Alvinactis*

Diagnosis. Pedal disc well developed. Column smooth, not divisible into scapus and scapulus, with distal row of verrucae and cinclides. Distal margin of column distinctly marked as marginal ring. Tentacles of uniform thickness along entire length, those of inner cycle longer than those of outer cycle. Longitudinal muscles of tentacles ectodermal, equally

developed. Mesenteries arranged in four cycles, only first cycle perfect. Same number of mesenteries proximally and distally. All mesenteries except those of youngest cycle fertile. Two well developed siphonoglyphs each attached to pair of directives. Retractor muscles diffuse; parietobasilar muscles not differentiated. Cnidom: Robust and gracile spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores.

Types species. *Alvinactis reu* sp. nov.

Etymology. The name *Alvinactis* combines the name of the submersible "Alvin" and "–actis" a common suffix for actiniarians, referring to their rayed or star-like external morphology.

***Alvinactis reu* sp. nov.**

(Figs 2-5, Table 2)

Diagnosis. Column of preserved specimens cylindrical, not divisible into scapus and scapulus, with more or less distinct marginal ring. Column smooth except for distal belt of small, round, perforate verrucae. Mesenteries hexamerously arranged in four cycles, all larger ones fertile, only those of first cycle perfect. Tentacles with numerous spirocysts and basitrichs; holotrichs in tips of tentacles of most specimens. Pedal disc diameter 14-59 mm, column height 6-34 mm (contracted and preserved specimens).

Material examined. FMNH 1150*, holotype; FMNH 11504, 3 paratypes.

Base and column. Column stout, of approximately equal diameter throughout in preserved specimens, encircled by distal belt of 24 small, hollow outgrowths of all three layers of column, perforate verrucae (Figs 2B, D, 4D, E). Verrucae inside crease beneath sphincter, associated with endocoelic spaces of stronger mesenteries, likely adherent. No fosse, although distal edge of column may extend over base of tentacles in contracted specimens

(Figs 2A, B). Column of preserved specimens uniform brownish-pink. In life, column trumpet shaped, flaring slightly from base (Fig. 3); column, tentacles, and oral disc of living specimens uniform translucent grayish-green. Strong columnar circular musculature and mesogleal sphincter; sphincter spans distal quarter of column, reticulated, lies closer to epidermis than gastrodermis, tapers more distally than proximally (Fig. 4E). Mesoglea of distal column with small, darkly-staining inclusions; these are especially abundant near marginal sphincter.

Base flat or slightly withdrawn inside column. Pedal disc adherent, muscular, same color as column in preserved material, approximately equal or slightly wider in diameter than oral disc in preserved specimens (Fig. 2A). Pedal disc circular in smaller specimens; oval in largest specimen.

Oral disc and tentacles. Tentacles marginal, approximately 100 in five cycles; those of outer cycle markedly shorter; those of inner cycles obscure oral disc in contracted specimens (Figs 2A, B). Specimens with more than 96 tentacles do not have additional mesenteries, suggesting tentacle regeneration rather than additional cycles of mesenteries at the distal column. Tips of tentacles perforated. Inner tentacles moderate in length, to 21 mm long, longitudinally sulcated in preserved specimens (Fig. 2B). In life, tentacles conical, approximately equal in length or longer than column. Oral disc flat, mouth oval; two prominent siphonoglyphs. Tentacles, oral disc, lips, actinopharynx, and siphonoglyphs same color as column.

Mesenteries and internal anatomy. Mesenteries arranged hexamerously in four cycles, those of first cycle perfect; two pairs of directives, each attached to a well developed siphonoglyph. All mesenteries of first, second, and third cycles (including directives) bear filaments and gametogenic tissue; those of fourth cycle weak, lacking filaments and gametogenic tissue (Fig. 4C). Species gonochoric; all specimens collected in late November

sexually mature, with either oocytes or spermatic vesicles (48-234 and 31-120 μm in diameter, respectively; Figs 4B, G).

Longitudinal muscles of mesenteries diffuse (Figs 4G, H). Pennon of parietobasilar muscles not differentiated (Fig. 4H). Basilar muscles present, equally developed (Fig. 4A).

Cnidom. Robust and gracile spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores (Fig. 5). See Table 2 for size and distribution.

Habitat and biology. All specimens living on and among oxidized clumps of the tubeworm *Tevnia* (Fig. 3). Multiple individuals co-occur on single clump, but specimens typically not close enough to touch one another.

Etymology. The specific name "*reu*" honors the NSF Research Experience for Undergraduates program, which supported CNC's participation in this project. The species epithet should be considered an undeclinable Latin noun.

Discussion

Comparison of *Alvinactis reu* gen., sp. nov. with other genera

As is true of other sea anemones described from chemosynthetic environments (e.g., Fautin and Hessler 1989; Fautin and Barber 1999; López-González *et al.* 2003, 2005), *Alvinactis* gen. nov. presents an unusual combination of characters that make it incompatible with the diagnoses of other genera. It has four cycles of mesenteries; although only those of the first cycle are perfect, all of the larger mesenteries are fertile. It has a belt of perforate verrucae encircling the distal column, and a strong circumferential marginal ring.

Our phylogenetic analysis demonstrates that *Alvinactis* gen. nov. is clearly part of the Actinosyphiidae, and lies within the Chemosynthina, but its relationship to other genera is unclear. In some of the primary trees, *Alvinactis* and *Paranthosactis* together are the sister

clade to a clade of *Cyananthea* and *Pacmanactis* because all have a marginal ring (#26). The marginal ring optimizes elsewhere on the tree, as a synapomorphy for *Hormosoma*, *Anthosactis janmayeni*, and *Tealidium*, and in *Bathydactylus* and in the outgroup *Kadosactis*. In other primary trees, *Alvinactis* and *Paranthosactis* are together (but not resolved) as the sister to *Maractis* and *Marianactis,* based on an imperfect second cycle of mesenteries (#12). *Alvinactis* gen. nov. is also associated with *Maractis* and *Pacmanactis* individually: as sister to *Maractis* because both lack microbasic *p*-mastigophores in the tentacles (#31), or as sister to *Pacmanactis* because both have a distal row of verrucae (#4).

The primary anatomical difference between *Alvinactis* gen. nov.*, Maractis*, *Marianactis*, and *Paranthosactis* is the distal belt of verrucae in *Alvinactis* gen. nov. Verrucae are hollow outgrowths of all three layers of the column; the ectodermal musculature and epidermis of verrucae differ from that of the surrounding column (Stephenson 1928, den Hartog 1987). These are most commonly seen in endomyarian sea anemones, in members of the family Actiniidae in particular (Stephenson 1928, Carlgren 1949, den Hartog 1987). The columnar outgrowths of acontiarian and mesomyarian anemones are typically called "suckers" or "tenaculi"; these structures are solid rather than hollow (Stephenson 1921). As the columnar structures of *Alvinactis* gen. nov. are hollow (Figs 4C, E), and are identical in form to verrucae of actiniid anemones (see, e.g., den Hartog 1987; Daly 2004), we consider them verrucae rather than suckers. Although there is no material adhering to the verrucae of *Alvinactis reu* gen., sp. nov., this is frequently the case in preserved specimens of species known to bear verrucae (MD, pers. obs.)

Alvinactis gen. nov. further differs from *Maractis* because the latter lacks a marginal ring, and from *Paranthosactis* because *Alvinactis* gen. nov. lacks microbasic *p*-mastigophores in the tentacles. In other actiniarians (e.g., Actiniidae, Edwardsiidae, Isanthidae, etc), having specializations like verrucae, tenaculi, or vesicles on the column is of generic significance

(Carlgren 1949). It is possible that it is of lesser significance among mesomyarians, and that *Alvinactis* gen. nov.*, Maractis,* and *Paranthosactis* belong in the same genus. However, because cladistic analysis of morphological data (including all the aforementioned similarities) did not consistently recover sister group relationships among these taxa, we have no objective basis for synonymizing them.

Alvinactis gen. nov., *Cyananthea, Pacmanactis,* and *Marianactis* are all known from chemosynthetically active habitats in the Pacific Ocean, but these three genera are clearly distinct. Like *Pacmanactis*, *Alvinactis* gen. nov. has distal perforate verrucae, although the distal structures are not histologically defined in *Pacmanactis* (López-González *et al.* 2005); they differ in that *Alvinactis* gen. nov. lacks microbasic *p*-mastigophores in the tentacles, and lacks microbasic *b*-mastigophores in the column margin and in the tentacles. Both *Pacmanactis* and *Cyananthea* have two cycles of perfect mesenteries, whereas *Alvinactis* gen. nov. has only one perfect cycle. Furthermore, *Cyananthea* has a distal belt of cinclides in the distal column but not verrucae. *Marianactis* has a distal belt of cinclides in the column and only one cycle of perfect mesenteries, characteristics seen in *Alvinactis* gen. nov. Nevertheless, *Marianactis* lacks both verrucae and a marginal ridge, lacks holotrichs in the distal column or tentacles, and has a differentiated pennon on the parietobasilar muscles. *Marianactis* also has microbasic amastigophores rather than microbasic *p*-mastigophores in the tentacles, but this distinction is of less value because of the difficulty of distinguishing between these nematocysts when undischarged (Östman 2000).

Phylogenetic relationships of Actinostolidae and Actinoscyphiidae

Our phylogenetic analysis of morphological data highlights problems with the taxonomy and organization of Actinostolidae in its old sense. Neither the strict consensus tree (Fig. 1) nor any of the primary trees support monophyly of Actinostolidae, suggesting that it

is a grade rather than a clade. Phylogenetic analysis of a more diverse assemblage of actiniarians, including representatives of *Actinostola*, *Actinoscyphia, Anthosactis, Hormosoma, Stomphia*, and the taxa used here as outgroups recovers a pattern of relationships compatible with the morphological evidence (Daly *et al.* 2008).

The sole feature shared by all members of Actinostolidae is a mesogleal marginal sphincter, an attribute common to many other actiniarian families. The remaining diagnostic features are absences: lack of the nematocyst-dense threads called acontia and of microcnemic mesenteries. The lack of resolution and the inclusion of *Actinoscyphia* and the outgroups *Bathyphellia, Hormathia,* and *Kadosactis* among the ingroup taxa suggest that some members of Actinostolidae are not closely related to one another; *Bathyphellia, Hormathia,* and *Kadosactis* belong to the superfamily Acontiaria. Molecular evidence suggests that all Acontiaria belong to a monophyletic group, although this clade also includes taxa without acontia (Daly *et al.* 2008). It is likely that at least some members of the family will need to be transferred to other families or placed in new families.

Nevertheless, our phylogenetic analysis indicates that some genera share uniquely derived attributes (Fig. 1). Our clade Actinostolina contains many of the taxa Carlgren (1899) included in his original description of the subfamily Actinostolinae, including the type genus *Actinostola*. Two synapomorphies for Actinostolina are characteristics Carlgren (1899) ascribed to the subfamily Actinostolinae, including mesogleal longitudinal muscles in tentacles (#23) and microbasic *b*-mastigophores in the tentacles (#30). The third feature, microbasic *p*-mastigophores in the tentacles (#31), has also been used to distinguish actinostolid genera (Carlgren 1949). Internal brooding of offspring (#35) is seen outside of Actinostolina only in *Anthosactis pearseae;* as *Anthosactis* is a polyphyletic assemblage, the interpretation of this character is unclear. Perfect mesenteries in the second and third cycles (#s 12, 13) characterize most members of the Actinostolina, except *A. janmayeni, Tealidium,*

and *Ophiodiscus*; in these three taxa, none of the mesenteries of the third cycle are perfect (#13).

Carlgren (1949) used the dissimilar morphology of mesenteries of a pair (#s 7, 8) to divide the actinostolids (groups I and II, see Carlgren 1949). These features are a synapomorphy for a clade within Actinostolina that encompasses most of the taxa Carlgren (1949) placed in group I (Fig.1). However, at least two genera (*Antholoba* and *Pycnanthus*) with similar mesenteries group with the clade of taxa with dissimilar mesenteries (Fig. 1). The tree provides no support for the monophyly of the taxa Carlgren (1949) placed in group II, although this is not surprising, as having paired mesenteries of similar morphology is common to most Actiniaria.

The genus *Anthosactis* is very heterogeneous, and previous authors have suggested that it may be a polyphyletic assemblage rather than monophyletic clade (e.g., Riemann-Zürneck 1997; White *et al.* 1999; Daly and Gusmão 2007). Our results bolster this interpretation: the three species of *Anthosactis* in our analysis did not group together, being widely dispersed through the tree. The type species *A. janmeyeni* groups with *Hormosoma* and *Tealidium* as the sister clade to Actinostolina (Fig. 1). A close relationship between *Tealidium* and *Anthosactis* has been proposed previously (Riemann-Zürneck 1997). Batteries of microbasic *b*-mastigophores in the aboral bases of the tentacles (#29) and the sphincter forming a marginal ring (#26) group *Hormosoma* and the clade comprised of *A. janmayeni* and *Tealidim*. The two other species of *Anthosactis*, *A. nomados* and *A. pearseae*, are in the other main clade: *A. pearseae* is the sister group to Chemosynthina, and *A. nomados* is the sister group to the crown clade consisting of Actinoscyphiidae and its sister clade.

In the consensus tree, *Epiparactis*, *Actinoscyphia*, and *Anthosactis pearseae* are sister to the clade we call Chemosynthina, and this clade is the sister to a group composed of *Hadalanthus, Bathydactylus,* and the acontiate outgroups. Although the clustering of

outgroup and ingroup taxa points to problems in the circumscription of these groups, some components of this tree have been advocated by other authors. In the discussion that accompanied her resurrection of family Actinoscyphiidae, Riemann-Zürneck (1978a) hypothesized a close relationship between *Epiparactis* and *Actinoscyphia*. Following Schmidt's (1972, 1974) subdivision of mesomyarians in "Early" and "Late" groups based on attributes of the cnidae, Rieman-Zürneck (1978a) further hypothesized that members of Actinoscyphiidae had lost acontia. Stephenson (1920) expressed a similar idea by including *Lilliella* Stephenson, 1918 and *Isoparactis* Stephenson, 1920 in Actinoscyphiidae; these genera have since been synonymized with the acontiate genera *Hormathia* and *Acraspedanthus* Carlgren, 1924, respectively. Sanamyan and Sanamyan (2007) considered *Cyananthea* and *Epiparactis* within Actinoscyphiidae, following the diagnosis given by Riemann-Zürneck (1978a). They also noted that the ring of cinclides in the distal column of *Cyananthea* strongly recalls *Kadosactis,* thereby relating *Cyananthea* to acontiarians. Finally, Sanamyan and Sanamyan (2007) pointed out the similarities between *Pacmanactis* and *Cyananthea* (both only differing in the presence of verrucae and the number of mesenteries distally and proximally), and highlighted the similarities in the cnidom of *Marianactis* and *Cyananthea*. Based on these comparisons, they proposed *Pacmanactis* and *Marianactis* be transferred to Actinoscyphiidae but they did not make the change (see Sanamyan and Sanamyan 2007).

In our consensus tree, most of the taxa Sanamyan and Sanamyan (2007) include in Actinoscyphiidae group together (Fig. 1). *Epiparactis* is basal to the rest of the genera of this clade. It lacks holotrichs in the tentacles (#33), a feature shared by all other taxa except *Marianactis*, and has three rather than four complete cycles of mesenteries. Most members of Actinoscyphiidae have a marginal sphincter situated closer to the epidermis (#27), and four cycles of mesenteries (#10). The Actinoscyphiidae is the sister to a clade that includes the

acontiarian outgroups plus *Hadalanthus* and *Bathydactylus*. Thus, this analysis suggests a close relationship between Actinoscyphiidae and some Acontiaria.

Within Actinoscyphiidae is Chemosynthina, the clade containing the genera reported from hydrothermal vents and cold seeps. *Anthosactis pearseae*, known from whalefalls, is the sister group to Chemosynthina in some but not all primary trees. Monophyly of Chemosynthina is supported by a mosaic of characters: the presence of cinclides (#5), relatively robust or thick column walls (#6, except *Pacmanactis* and *Marianactis*), equal numbers of mesenteries proximally and distally (#9, except *Cyananthea*), fertile mesenteries in the third cycle (#17, except *Pacmanactis*), a strong sphincter (#25, except *Pacmanactis*), a marginal ring (# 26, absent in *Maractis* and *Marianactis*), and microbasic *p*-mastigophores in the tentacles (# 31, except *Maractis* and *Alvinactis* gen. nov.). In our re-examination of the type material of *Marianactis,* we found a belt of small cinclides in the distal column; the cinclides are very small and are inconspicuous in preserved material, and are therefore easily overlooked. Their presence may also have been overlooked in *Maractis* or *Paranthosactis*.

Based on these results, we accept Sanamyan and Sanamyan's (2007) circumscription of Actinoscyphiidae, and add to it *Marianactis* and *Pacmanactis*, *Alvinactis* gen. nov., *Maractis*, and *Paranthosactis*. Actinostolidae in a new sense includes the genera in Actinostolina, plus an assemblage of taxa that are basal to Actinostolina or Actinosyphiidae, including *Anthosactis*, *Antiparactis*, *Cnidanthea*, *Cnidanthus*, *Hormosoma*, *Paranthus*, *Pseudoparactis,* and *Tealidium*. Actinostolidae in its new sense is not monophyletic. Re-organizing it to reflect monophyly will require dense sampling across Actiniaria, and should include molecular as well as morphological data. *Anthosactis* is polyphyletic, with some members more closely related to genera in Actinoscyphiidae than to those in Actinostolidae. Because the type species *A. janmayeni* lies within Actinostolidae, pending a comprehensive species-level revision of *Anthosactis*, we leave it in Actinostolidae.

In addition to identifying potential synapomorphies for Actinoscyphiidae, Actinostolidae, and their subgroups, our analysis highlights characters that seem to have little ability to group taxa. The number of distal and proximal mesenteries (#9) varies widely in the family, and has not been assessed for many taxa. Similarly, having the sphincter form a marginal ring (#26) occurs quite broadly across the tree, as do broad bathymetric ranges (#37). As with the number of mesenteries, these features may have been scored inconsistently by some authors, making them appear less informative than they actually are. The relative thickness of the column wall (#6) is often not recorded and is very subjective, varying with degree of contraction and preservation state.

The types of nematocysts in the tentacles have been used as a generic character in Actinostolidae (Carlgren 1949; Fautin and Hessler 1989). The presence of microbasic *b*-mastigophores is a potential synapomorphy of Actinostolina; their presence and arrangement in batteries distinguishes *Tealidium, Hormosoma*, and *Anthosactis* (see Carlgren 1949). However, the use of these features as taxonomic characters has been challenged in recent studies (see López-González *et al.* 2003). Similarly, although microbasic *p*-mastigophores or amastigophores have been used to differentiate actinostolid genera, the phylogenetic value of these characters is far from clear because these types are difficult to distinguish with light microscopy (Östman 2000). Holotrichs in the tentacles are inducible in some species (e.g., Fautin 1988; Edmands and Fautin 1991), rendering them suspect as a taxonomic or phylogenetic feature. Nonetheless, holotrichs in the tentacles is phylogentically useful in this analysis, grouping Chemosynthina and its allies.

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Table 1. Synthesis of the taxonomic history of the families Actinostolidae and Actinoscyphiidae. Names are written as given in the original publication, with current valid names given in brackets. First use of suprageneric names in bold.

Year	Author	Family	Subfamilies	Genera (when given)
1882	Hertwig	**Paractidae**		*Antholoba, Dysactis, Ophiodiscus, Paractis, Tealidium*
1883	Andres	Actininae	Paractidae	*Paranthus, Paractis, Paractinia*
1893	McMurrich	Paractidae		*Actinernus* [*Actinoscyphia*], *Actinostola, Antholoba, Cymbactis* [*Paractinostola*], *Ophiodiscus, Paractis, Paranthus, Paractinia, Pycnanthus, Tealidium*
1893	Carlgren	Paractidae		*Antholoba, Kadosactis, Kyathactis* [*Actinostola*], *Ophiodiscus, Paractinia, Paractis, Paranthus, Tealidium*
		Actinostolidae		*Actinostola, Stomphia*
1899	Carlgren	Paractidae	**Actinostolinae**	*Actinostola, Stomphia*
			Paractinae	*Antholoba, Ophiodiscus, Paractis, Paranthus, Tealidium*
1918	Carlgren	Paractidae	Paractinae	
			Actinostolinae	
			Polysiphoniidae (Exocoelactiidae)	*Polysiphonia* [*Exocoelactis*]
1920	Stephenson	**Actinosyphiidae**		*Actinoscyphia, Paranthus, Isoparactis* [*Acraspedanthus*], *Lilliella* [*Hormathia*]?
1921	Stephenson	Paractidae	Paractinae, Actinostolinae, Polysiphoniinae	*Actinostola, Antholoba, Anthosactis, Hormosoma, Exocoelactis, Ophiodiscus, Paractis,* [*Cnidanthus, Paractinostola, Parasycionis, Pycnanthus, Stomphia, Sycionis*], *Paranthus, Tealidium*
1932	Carlgren	Actinostolidae		*Actinostola, Anthosactis, Pycnanthus, Stomphia*
1949	Carlgren	Actinostolidae		*Actinostola*, *Actinoscyphia, Antholoba*, *Anthosactis, Antiparactis*, *Bathydactylus*, *Cnidanthus*, *Isoparactis*, *Epiparactis, Hormosoma*, *Ophiodiscus*, *Paractinostola*, *Paranthus*, *Parasicyonis, Pseudoparactis*, *Pycnanthus*, *Sicyonis*, *Stomphia*, *Synsicyonis, Tealidium*
1978	Riemann-Zürneck	Actinoscyphiidae		*Actinosyphia, Epiparactis*
2007	Sanamyan and Sanamyan	Actinoscyphiidae		*Actinosyphia, Cyananthea, Epiparactis, Marianactis* ?, *Pacmanactis* ?

Table 2. Summary of size ranges of cnidae of *Alvinactis reu* gen., sp. nov. "Sample" indicates the number of specimens in which each cnidae was found out compared to the number of specimens examined; "N" indicates the total number of capsules measured; "F" is the relative frequency of each type of capsule in that tissue: +++ = very common, ++ = common, + = less common, --- = sporadic. "$\overline{X}$" is the average size of a capsule, and "SD" the standard deviation of the measured samples; values from pooled samples.

Category	Sample	N	F	Range of length and width of capsules (µm)	$\overline{X}$ ± SD
PEDAL DISC					
Basitrichs	4:4	64	++	(17.6-29.7) x (1.0-3.3)	22.9 ± 3.0 x 2.2 ± 0.4
SCAPUS					
Basitrichs	4:4	60	+++	(19.2-29.5) x (1.5-3.2)	23.85 ± 2.3 x 2.4 ± 0.4
Microbasic *p*-mastigophores				not seen	
MARGIN					
Basitrichs	4:4	60	+++	(18.8-31.6) x (1.6-3.1)	25.5 ± 2.7 x 2.5 ± 0.4
Microbasic *p*-mastigophores	4:4	40	+/++	(24.6-37.6) x (3.5-6.1)	30.1 ± 2.7 x 4.6 ± 0.6
Holotrichs	2:4	6	---/+	(18.6-25.4) x (3.0-3.7)	21.5 ± 2.8 x 3.2 ± 0.3*
OUTER TENTACLE BASE					
Robust spirocysts	4:4	60	++	(18.7-47.4) x (2.3-7.2)	28.6 ± 6.8 x 4.5 ± 1.2
Basitrichs	4:4	61	+++	(16.4-35.6) x (1.2-3.2)	28.5 ± 3.3 x 2.3 ± 0.5
Holotrichs				not seen	
TENTACLE TIP					
Robust spirocysts	4:4	80	++/+++	(16.1-59.5) x (2.2-7.8)	32.2 ± 9.9 x 3.9 ± 1.1
Basitrichs	4:4	110	+++	(13.9-38.6) x (1.3-3.4)	30.7 ± 5.6 x 2.4 ± 0.5
Holotrichs	3:4	26	---/+	(21.4-38.4) x (4.5-8.2)	30.8 ± 4.5 x 6.1 ± 0.8*
ACTINOPHARYNX					
Basitrichs	3:3	23	---/+	(17.2-37.2) x (1.1-3.4)	30.3 ± 3.9 x 2.4 ± 0.6*
Microbasic *p*-mastigophores	3:3	60	+++	(27.3-39.4) x (3.5-5.8)	34.4 ± 2.2 x 4.7 ± 0.6
FILAMENTS					
Basitrichs	3:3	44	+/++	(13.2-33.3) x (1.2-4.1)	21.4 ± 4.9 x 2.2 ± 0.5
Microbasic *p*-mastigophores	3:3	60	+++	(28.0-39.4) x (3.0-5.8)	32.9 ± 2.5 x 4.5 ± 0.5

(*) Average based on fewer than 40 capsules; the measurement of at least 40 capsules is the minimum sufficient for statistical significance (Williams 1998, 2000).

Figure Legend

Fig. 1. Strict consensus of 22 equally parsimonious trees (L=167, CI=0.29, RI=0.59) recovered from analysis of morphological data (Appendix 2). Numbers above the branches are Bremer support values. Characters supporting Actinostolina, Actinoscyphiidae, and Chemosynthina are indicated; numbers refer to Appendix 1.

Fig. 2. External anatomy, preserved specimens *Alvinactis reu* gen., sp. nov. Scale in mm. A. Lateral view. B. Close up of column margin. Note verrucae inside crease in distal column (arrows). C. Top view. D. Perforate verrucae.

Fig. 3. External anatomy and habitat, living *Alvinactis reu* gen., sp. nov.

Fig. 4. Internal anatomy and histology, *Alvinactis reu* gen., sp. nov. Scale in μm. A. Basilar muscles. B. Cross-section through a tentacle of a contracted individual. Note gametogenic tissue in coelenteric space of tentacle. C. Longitudinal section through verrucae in distal column. D. Cross section through mesenteries below actinopharynx, showing size dimorphism of mesenteries if the first and third cycles. E. Longitudinal section through distal column, showing mesogleal sphincter and verruca (arrow). The space separating the distal and proximal portions of the sphincter is not present in all specimens or all sections from a single specimen. F. Maturing oocyte with trophonema (arrow). G. Cross section through parietal muscle of larger mesentery. H. Cross section through mesenteries below actinopharynx, showing diffuse retractor musculature. Abbreviations: ep, epidermis; ga, gastrodermis.

Fig. 5. Cnidae of *Alvinactis reu* gen., sp. nov. A. Basitrich. B. Basitrich. C. Basitrich. D. Microbasic *p*-mastigophore. E. Gracile spirocyst. F. Basitrich. G. Holotrich. H. Robust spirocyst. I. Basitrich. J. Basitrich. K. Microbasic *p*-mastigophore. L. Basitrich. M. Microbasic *p*-mastigophore.

Appendix 1. Morphological characters used in cladistic analysis of Actinostolidae. Characters in bold used in Carlgren's 1949 key to the actinostolid genera. Characters that do not manifest exclusive states in all members of a taxon have been broken into several binary characters (e.g., #s 22 and 23) rather than coded as single multistate characters. Characters applicable only to outgroup taxa indicated.

External anatomy

0. Column regions: absent (0); scapus/scapulus present (1).

1. Column surface: smooth (0); mesogleal papillae present (1).

2. Column with cuticle: absent (0); present (1).

3. Column with tenaculi: absent (0); present (1).

4. Distal verrucae on column: absent (0); present (1).

5. Distal cinclides on column: absent (0); present (1).

6. Column mesoglea: thin (0); thick (1).

Internal anatomy

7. Mesenteries of a pair equally developed: yes (0); no (1).

8. Muscles of larger mesentery of an unequal pair (from 7): facing the nearest mesentery of preceding cycle (0); facing both preceding and ante-preceding cycle (1).

9. Number of distal *vs* proximal mesenteries: fewer (0); same (1); more (2).

10. Maximum number of cycles of mesenteries: three cycles (0); four cycles (1); five cycles (2); six cycles (3); seven cycles (4).

11. Perfect mesenteries in first cycle: absent (0); present (1).

12. Second cycle of mesenteries perfect: none (0); some (1); all (2).

13. Third cycle of mesenteries perfect: none mesenteries (0); some mesenteries (1); all mesenteries (2).

14. Forth cycle of mesenteries perfect: none (0); some (1); all (2); non applicable (-).

15. Fertile first mesentery cycle: absent (0); present (1).

16. Fertile second mesentery cycle: absent (0); present (1).

17. Fertile third mesentery cycle: absent (0); present (1).

18. Smallest mesentery cycle fertile: absent (0); present (1).

19. Dimorphic, filament-free fertile and filament-bearing sterile mesenteries: absent (0); present (1).

20. Basal tentacle mesoglea: not thickened (0); thickened (1).

21. Development of longitudinal tentacles muscles: similar (0); more developed on the oral side (1).

22. Ectodermal longitudinal tentacle muscles: absent (0); present (1).

23. Mesogleal longitudinal tentacle muscles: absent (0); present (1).

24. Sphincter: mesogleal (0); endodermal (1).

25. Sphincter development: weak (0); strong (1).

26. Sphincter forming a marginal ring: absent (0); present (1).

27. Sphincter position in mesoglea: closer to gastrodermis (0); closer to epidermis (1); centred (2).
28. Parietobasilar muscles: not distinctly marked nor differentiated as a separate lamella (0); distinctly marked but without forming a separate lamella (1); differentiated as a separate lamella (2).

Tentacle cnidae

29. Batteries of microbasic *b*-mastigophores on basal, aboral side of outer tentacles: absent (0); present (1).

30. Microbasic *b*-mastigophores in the tentacles: absent (0); present (1).

31. Microbasic *p*-mastigophores in the tentacles: absent (0); present (1).
32. Basitrichs in the tentacles: absent (0); present (1).
33. Holotrichs in the tentacles: absent (0); present (1).
34. Robust spirocysts: absent (0); present (1).

Ecology and life history

35. Internal brooding: absent (0); present (1).
36. Deep sea: absent (0); present (1).
37. Shallow: absent (0); present (1).
38. Occurs in chemosynthetic habitats: no (0); yes (1).
39. Type of chemosynthetic habitat: vent (0); seeps (1); whale falls (2); non applicable (-).

Character for outgroup genera

40. Acontia: absent (0); present (1).

Appendix 2: Morphological character state distributions for outgroups and ingroups genera. Dash indicates that the corresponding state is unknown or inapplicable. Outgroup genera in bold. See appendix 1 for character list.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Actinoscyphia	0	0	0	0	0		1	0		-	1	2	1	2	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0	-	0
Bathyphellia	1	1	1	1	0		-	0		-	0	0	1	0	0	-	1	0	0	0	0	0	0	1	0	0	1	0	2	2	0	0	0	1	0	1	0	1	0	0	-	1
Epiactis	0	1	0	0	0		0	0		-	0	2	1	2	2	0	1	1	1	0	0	0	0	1	0	1	1	0	-	2	0	0	1	0	0	0	1	1	1	0	-	0
Hormathia	1	1	1	0	0		1	0		-	1	1	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	-	1
Kadosactis	1	1	1	1	0		1	0		-	1	0	1	2	0	-	1	1	0	0	0	1	-	1	0	0	1	1	0	1	0	0	1	1	0	1	0	1	0	0	-	1
Actinostola	0	0	0	0	0		0	1		1	0	0	4	1	2	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	1	1	1	0	-	0
Alvinactis	0	0	0	0	1		1	0		-	1	1	1	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1	1	0	1	0	1	0	0
Antholoba	0	0	0	0	0		1	0		-	2	4	1	2	2	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	-	0
Anthosactis janmayeni	0	0	0	0	0		1	0		-	-	1	1	1	0	0	1	1	1	1	0	-	1	1	0	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	-	0
Anthosactis nomados	0	0	0	0	0		0	0		-	0	0	1	2	0	-	1	1	0	0	0	0	-	1	0	0	1	0	2	-	-	1	0	1	0	1	0	1	0	0	-	0
Anthosactis pearseae	0	0	0	0	0		1	0		-	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	2	0
Antiparactis	0	0	0	0	0		0	0		-	0	1	1	0	0	0	0	1	1	0	0	-	0	1	0	0	1	0	2	0	0	-	-	-	-	0	0	0	1	0	-	0
Bathydactylus	1	0	0	0	0		1	0		-	0	0	1	0	0	-	1	1	0	0	0	0	0	1	0	0	1	1	-	1	0	0	0	1	0	0	0	1	0	-	-	0
Cnidanthea	0	1	0	0	0		-	0		-	1	0	1	0	0	-	1	1	0	0	0	0	0	1	0	0	1	0	2	0	0	0	1	1	0	-	0	0	1	0	-	0
Cnidanthus	0	0	0	0	0		0	0		-	0	1	1	2	1	0	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	-	1	0	1	0	-	0
Cyananthea	0	0	0	0	0		1	0		-	2	2	1	2	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	0	0
Epiparactis	0	0	0	0	0		1	0		-	-	2	1	0	0	0	-	-	-	-	0	0	0	1	0	0	0	0	2	0	0	0	0	1	0	1	0	1	0	0	-	0
Hadalanthus	1	1	1	1	0		0	0		-	1	1	1	0	0	0	1	1	-	-	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	-	0	1	0	-	-	0
Hormosoma	0	0	0	0	0		1	0		-	1	1	1	2	2	0	1	1	1	1	0	0	0	0	1	0	1	1	1	2	1	1	0	0	0	0	1	0	1	0	-	0
Maractis	0	0	0	0	0		0	0		-	1	1	1	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	1	0	0
Marianactis	0	0	0	0	0		1	1		-	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	0	2	0	0	1	1	0	1	0	1	0	1	0	0
Ophiodiscus	0	0	0	0	0		1	1		0	-	1	1	2	0	0	0	0	0	1	1	1	1	0	1	0	0	0	-	0	-	-	-	-	-	-	0	1	0	-	-	0
Pacmanactis	0	0	0	0	1		1	0		-	1	1	1	2	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	1	1	1	1	1	0	1	0	1	0	0
Paractinostola	0	0	0	0	0		1	1		0	2	4	1	2	2	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	-	0	1	1	0	-	0
Paranthosactis	0	0	0	0	0		-	0		0	-	1	1	1	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	0	0
Paranthus	0	0	0	0	1		0	0		-	0	-	2	1	1	2	0	0	1	1	0	0	0	-	-	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	-	0
Parasicyonis	0	0	0	0	0		1	1		1	0	2	1	2	2	1	0	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	-	0	1	0	0	-	0
Pseudoparactis	1	0	0	0	0		-	0		-	-	1	-	-	-	-	0	1	1	-	0	-	-	1	0	0	0	0	2	0	-	-	-	-	-	-	0	0	1	0	-	0
Pycnanthus	0	0	0	0	0		1	0		-	0	2	1	2	1	0	0	0	1	1	0	1	1	0	1	0	1	0	0	1	0	1	1	1	0	0	1	1	0	0	-	0
Sicyonis	0	0	0	0	0		1	1		1	0	3	1	2	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	-	0
Stomphia	0	0	0	0	0		1	1		0	0	1	1	2	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	0	1	1	1	0	-	0
Synsicyonis	0	0	0	0	0		1	1		1	2	1	1	2	1	0	0	0	1	1	0	1	1	0	1	0	0	0	-	-	-	-	-	-	-	-	-	0	1	0	0	-	0
Tealidium	1	1	0	0	0		1	0		-	-	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	0	1	1	2	0	1	1	0	1	0	-	0	1	0	0	-	0

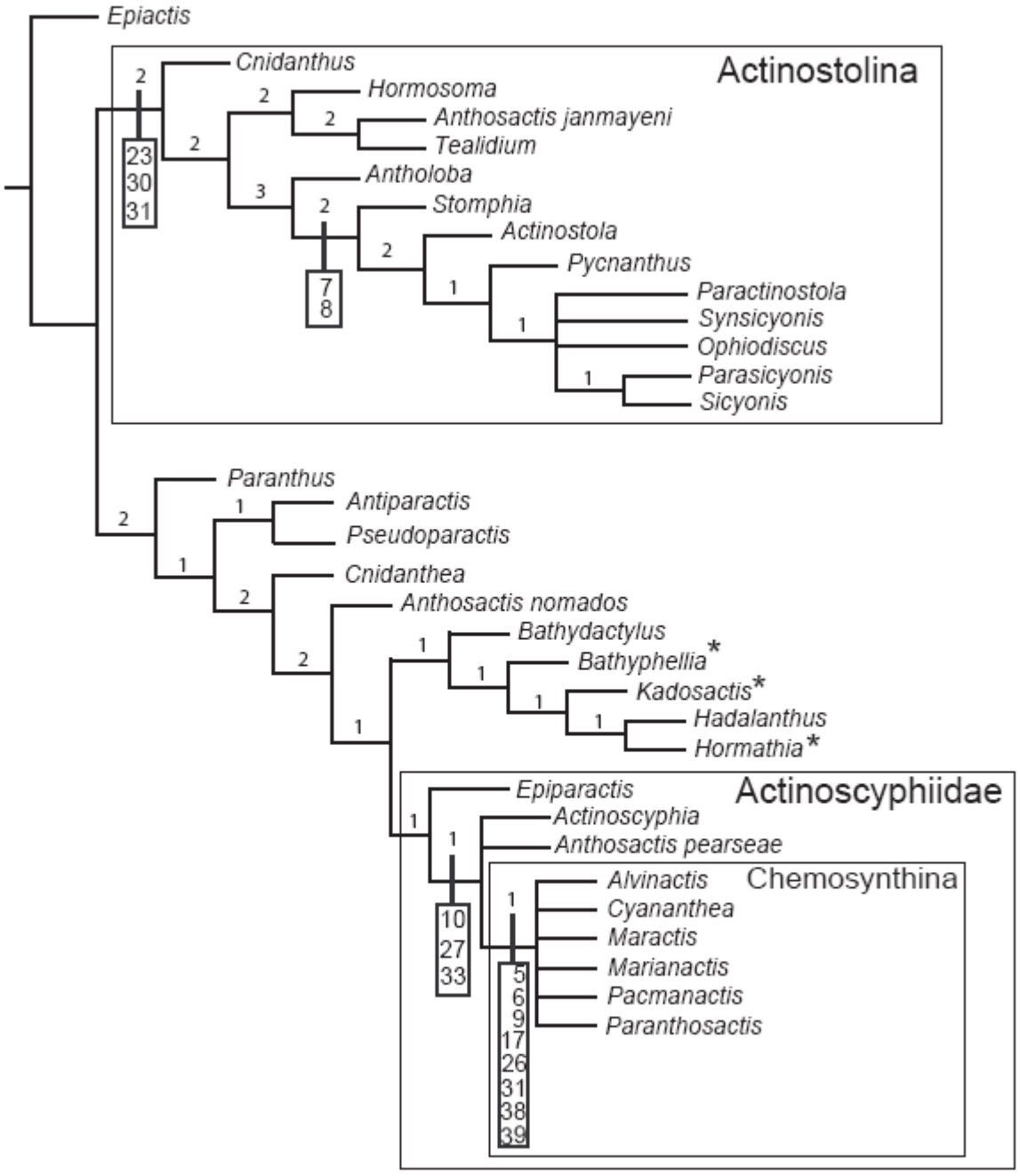
Epiactis
Actinostolina
Cnidanthus
Hormosoma
Anthosactis janmayeni
Tealidium
Antholoba
Stomphia
Actinostola
Pycnanthus
Paractinostola
Synsicyonis
Ophiodiscus
Parasicyonis
Sicyonis
Paranthus
Antiparactis
Pseudoparactis
Cnidanthea
Anthosactis nomados
Bathydactylus
Bathyphellia*
Kadosactis*
Hadalanthus
Hormathia*
Actinoscyphiidae
Epiparactis
Actinoscyphia
Anthosactis pearseae
Chemosynthina
Alvinactis
Cyananthea
Maractis
Marianactis
Pacmanactis
Paranthosactis

Figure 1.

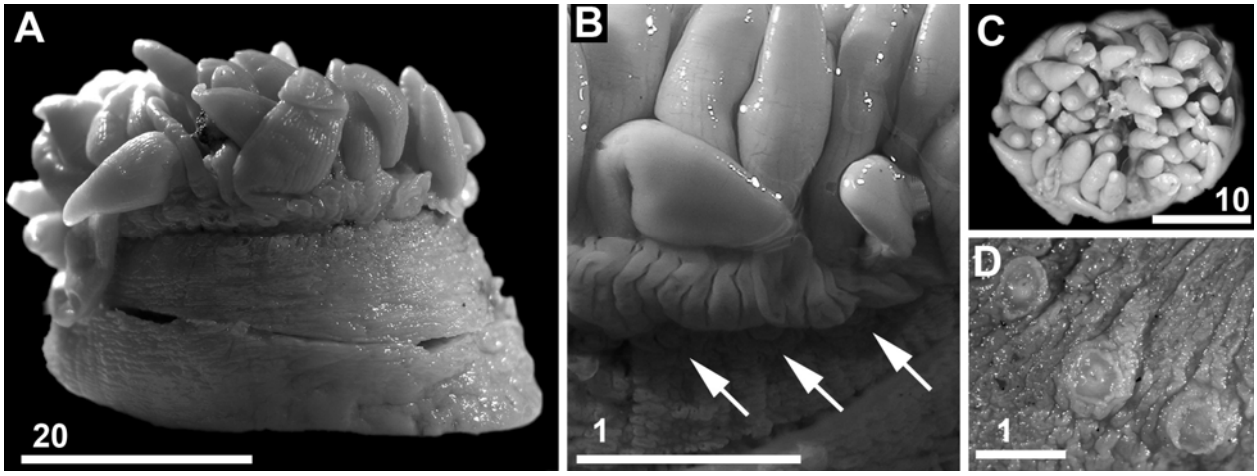

Figure 2.

Figure 3.

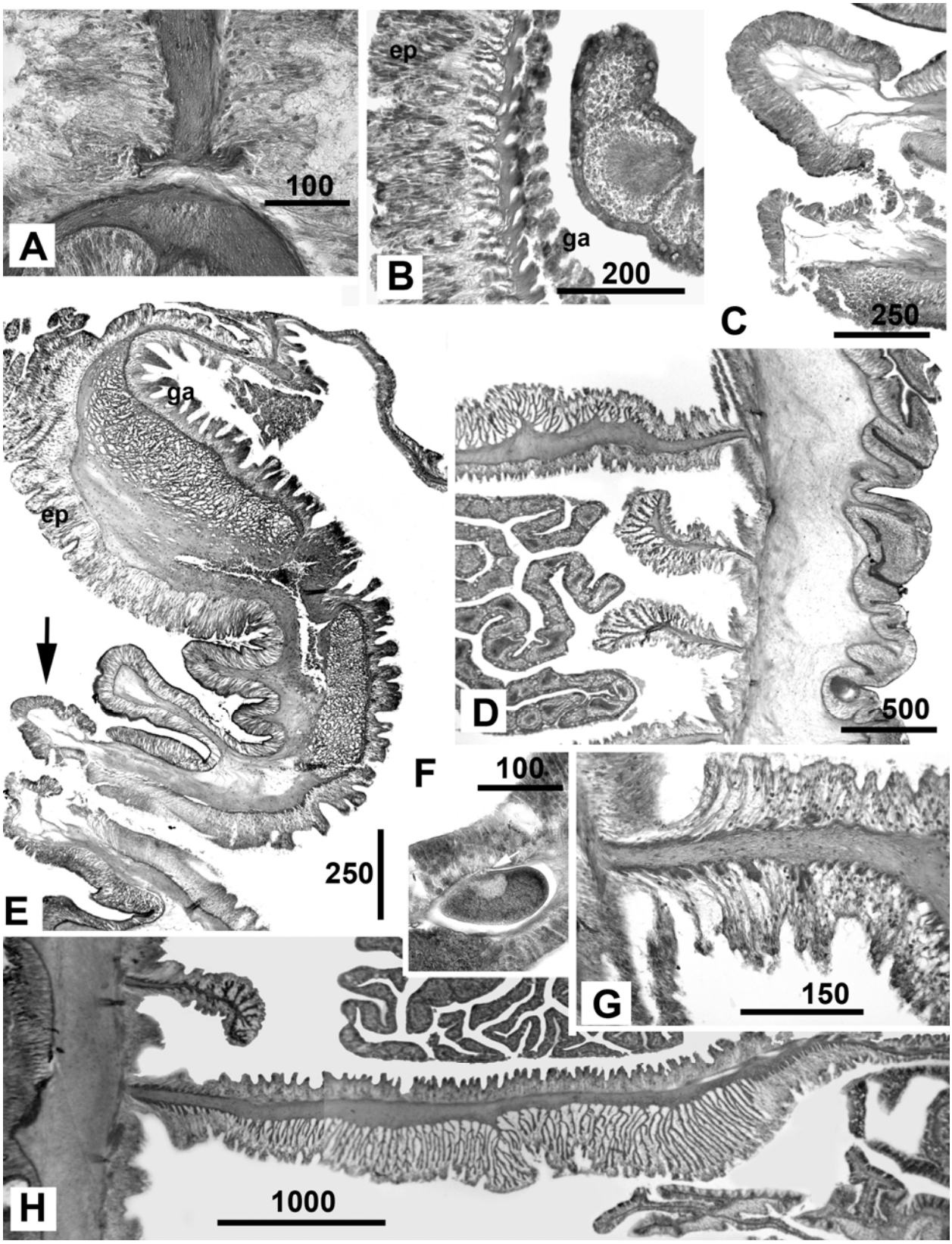

Figure 4.

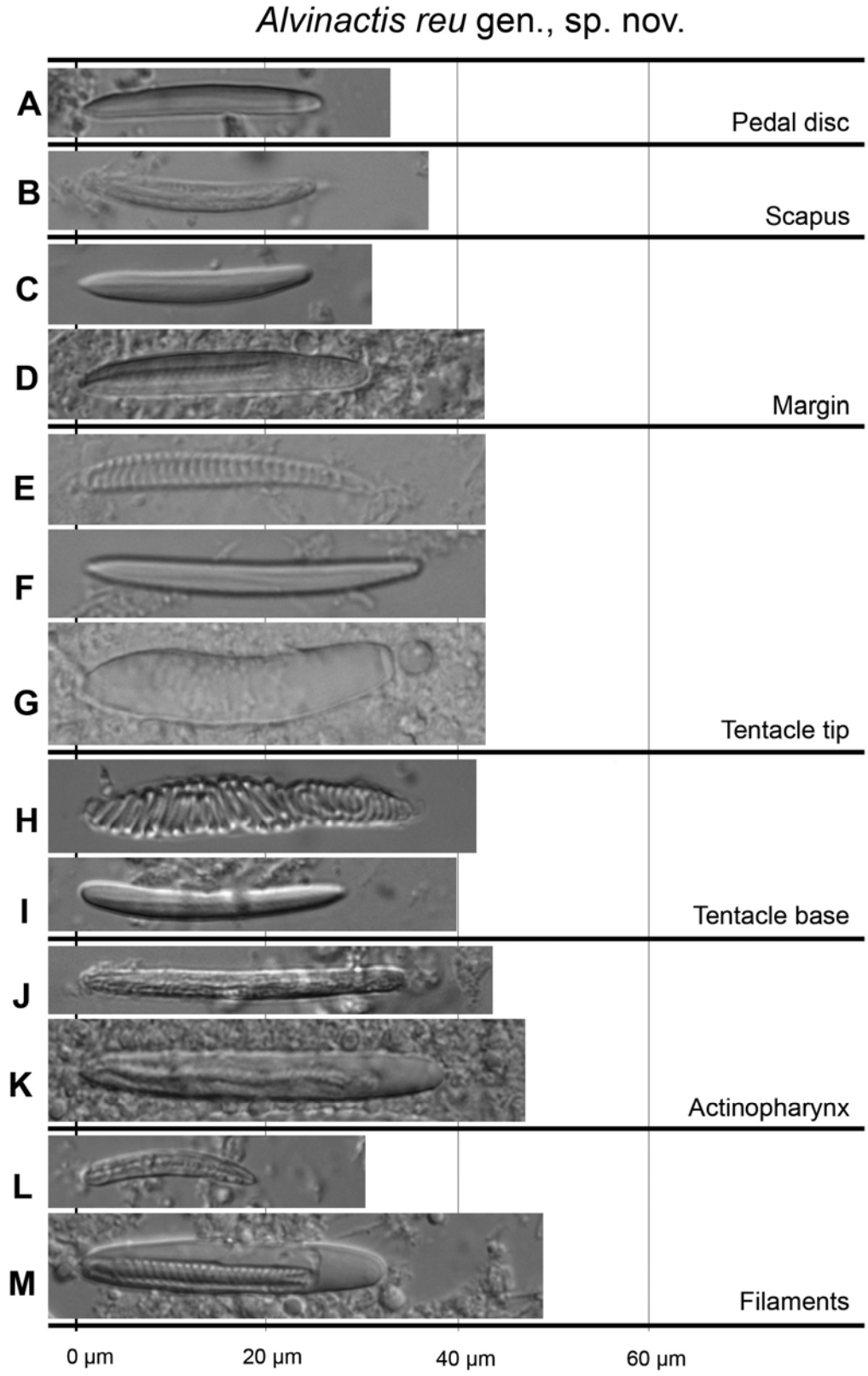
Alvinactis reu gen., sp. nov.
A
B
C
D
E
F
G
H
I
J
K
L
M
Pedal disc
Scapus
Margin
Tentacle tip
Tentacle base
Actinopharynx
Filaments
0 µm
20 µm
40 µm
60 µm

Figure 5.